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Population-specific social dynamics in chimpanzees

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Abstract

Understanding intraspecific variation in sociality is essential for characterizing the flexibility and evolution of social systems, yet its study in non-human animals is rare. Here, we investigated whether chimpanzees exhibit population-level differences in sociality that cannot be easily explained by differences in genetics or ecology. We compared social proximity and grooming tendencies across four semi-wild populations of chimpanzees living in the same ecological environment over three consecutive years, using both linear mixed models and social network analysis. Results indicated temporally-stable, population-level differences in dyadic-level sociality. Moreover, group cohesion measures capturing network characteristics beyond dyadic interactions (clustering, modularity and social differentiation) showed population-level differences consistent with the dyadic indices. Subsequently, we explored whether the observed intraspecific variation in sociality could be attributed to cultural processes by ruling out alternative sources of variation including the influences of ecology, genetics, and differences in population demographics. We conclude that substantial variation in social behavior exists across neighboring populations of chimpanzees and that this variation is in part shaped by cultural processes.

Significance Statement:

To understand species-typical behavior and enable valid cross-species comparisons, the range of within-species variation needs to be charted. Here, we investigated the extent of population-level variation in sociality across four neighboring populations of chimpanzees. Using standardized methodology, we report substantial differences in social affiliation and cohesion between these populations. The differences were stable across time and robust against variation in group size and the number of family units. Moreover, the observed differences could not be explained by variation in subspecies or ecology. We conclude that chimpanzee populations exhibit variability in sociality and that assessments of "chimpanzee-typical" behavior – be it for within-species studies or for larger-scale investigations of the evolutionary roots of human behavior – should consider this between-population variation.

What is a typical chimpanzee like? How is it similar to or different from a typical human? To answer these questions, it is fundamental to consider and account for the variability across individuals and populations within each species. While this logic is recognized for humans, there is a paucity of scientific focus on intraspecific variation in non-human animals. In this paper, we provide an account of population-level variation of social behavior in one of humans' closest living relatives – the chimpanzee.

Intraspecific, population-level variation in sociality may stem from a variety of factors, including genetic differences at the subspecies level, differences in ecological environments, differences in demographic makeup, and differences in individual temperaments (1–4). For non-human primates (henceforth: primates) in particular, socio-ecological theory was developed in order to understand and predict variation in social organization and behavior. This theory postulates that the structure of primate social organizations, emerging from the relationships among their members, can be understood as ecologically and phylogenetically determined (5–11).

With the advent of cultural primatology (12–16), and the identification of numerous learned behavioral differences across groups in great apes (17–21) and monkeys (22–24), the propensity of primates to develop population-specific behaviors has been well established (but see (25)). These behavioral differences extend beyond material culture to "social conventions" or "traditions" without apparent function (20, 21, 24, 26–30). Consequently, it seems conceivable that intraspecific, population-level differences in general sociality (e.g., interaction tendencies) could also emerge by means of learning processes, hence extending the ecological and phylogenetic determinism of sociality postulated by socio-ecological theory. Based on the current status of cultural primatology, or the study of culture in non-human animals more generally, we view this as a pressing question in the study of psychological and behavioral diversity: beyond isolated accounts of tradition formation in non-human animals, is there any indication that non-human animals exhibit intraspecific population-level variation in their everyday social interactions that might be instigated by cultural processes?

One seminal case demonstrating to the plausibility of learned, population-level differences in sociality was reported by Sapolsky and Share (31) in their study of olive baboons (*Papio anubis*). When a substantial portion of dominant baboon males had died from tuberculosis, the remaining troop was characterized by atypically low levels of aggression and high levels of affiliation ((31) also see (32)). If the baboons' interaction-styles would have been merely contingent on genetics, ecology and individual learning, the sudden alteration in

troop-level behavioral characteristics would have converged back to olive baboon-typical behavioral phenotypes over time. Instead, the atypical interaction-style became the new troop-level phenotype, which lead the authors to argue for the existence of nonhuman primate social culture (31, 32).

The possibility that intraspecific variation in primate sociality may in part emerge through social learning has been explored experimentally in marmosets (3, 33) and chimpanzees (28). In response to prerecorded affiliative calls of familiar conspecifics, marmosets were found to temporarily increase their overall levels of affiliative behavior (33). In another study, the same species was shown to exhibit group-level differences in individual boldness produced by social effects (3). Chimpanzees were observed to differ at a population level in the extent to which they tolerated each other's presence around valuable food resources (28). These experimental studies opened up the possibility that the observed behavioral patterns might be best explained in terms of local cultures, although alternative explanations could not be ruled out.

Here, for the first time, we investigate differences in sociality across neighboring chimpanzee populations with the specific purpose to identify a cultural signature in naturally-occurring variation in sociality by ruling out several alternative explanations. Specifically, we examine behaviors representative of chimpanzees' general level of sociality, i.e., spatial proximity and grooming, for possible population-level differences and assess the likelihood that any observed differences could be traced back to socially-learned templates of within-group interaction styles. In doing so, we acknowledge the intricate connection between ecology and culture (e.g., (34)), but follow the reasoning that *i*) this connection is less clear in the realm of social interaction-patterns (cf. socio-ecological theory) compared to the technological domain (i.e., tool use) (20), and *ii*) when ecology can be controlled for adequately, any remaining population-level variation requires an explanation.

First, we describe a unique testbed comprising several chimpanzee populations within the same ecological environment (i.e., ruling out ecological influences on behavior such as food availability and predation risk). Second, for two populations, we consider subspecies for each individual and assess the scope of its potential influence on inducing population differences in social behavior (i.e., ruling out genetically anchored subspecies-typical behavior). Third, we employ the same data-collection procedure across all four neighboring chimpanzee populations (i.e., ruling out methodological interference of the population difference analysis: (35)), and control for key demographic variables affecting chimpanzees' social dynamics in our statistical models (e.g., population size and number of kin). Lastly, we

use generalized linear mixed models and social network analysis in order to assess the nature of dyadic and population-level sociality, respectively.

Results

Party size. The size of congregations was significantly different between the four chimpanzee populations across the sampling period (LRT population: $\chi^2 = 32.4$, df = 1, $p < 0.0001$; Figure 1). Note that this effect emerged after controlling for population size, which did not significantly influence party size ($\chi^2 = 0.16$, df = 1, $p = 0.69$). Mean ± SD party sizes for populations 1–4 are given in Table S1. Moreover, the tendency to congregate in parties of specific sizes was a stable population-level feature across time, as indicated by the absence of a significant interaction between year and population (LRT year|population: $\chi^2 = 2.82$, df = 2, $p = 0.244$). None of the other variables predicted party size (all NS).

Matched population comparison. Populations 3 and 4 closely matched in demography and subspecies (see Table S2), yet organized themselves in congregations of different sizes each year (Welch 2-sample *t*-test, 2011: $t = -4.02$, df = 222, $p < 0.0001$; 2012: $t = -9.18$, df = 876.7, $p < 0.0001$; 2013: $t = -4.55$, df = 166.3, $p < 0.0001$; see Figure 1).

Association indices.

Proximity. The *probability* for two population members to have associated in close proximity over the course of the study period significantly differed across populations (Binomial part LRT for "population": $\chi^2 = 37.29$, df = 1, $p < 0.0001$). Whereas in the two smaller populations, each possible dyad was observed to be in proximity at least once, in the two larger populations there were dyads who never associated (population 1: ~15% of possible dyads; population 2: ~41% of possible dyads). In order to understand this pattern better, we re-ran the analysis with population size as fixed effect (instead of offset term), finding that the population difference in proximity probability could be explained by differences in population size (LRT "population size": $\chi^2 = 10.29$, df = 1, $p < 0.002$; estimate ± SD = -4.30 ± 2.73; LRT "population": $\chi^2 = 0.01$, df = 1, $p = 0.98$). This may be interpreted in terms of an inability to form social bonds with all individuals in large populations, not necessarily in terms of relatively low propensities to be in proximity to others. Furthermore, dyads' age ($\chi^2 = 6.69$, df

155 = 2, $p = 0.035$) and family configuration ($\chi^2 = 44.59$, df = 1, $p < 0.0001$) significantly affected
156 subjects' likelihood to associate, with adults being more likely to associate than dyads
157 including sub-adults (estimate ± SD: adult-adult versus adult-subadult: -1.08 ± 0.45, $p =$
158 0.016; adult-adult versus subadult-subadult: -1.45 ± 0.79, $p = 0.067$), and relatives being more
159 likely to associate than non-relatives (estimate ± SD: 3.15 ± 0.60, $p < 0.0001$). Dyads
160 consisting of different configurations with respect to "origin" (wild or captive born) and "sex"
161 did not vary in their probability to be in proximity.
162 The *extent* of associating within dyads was significantly affected by population
163 identity, while controlling for population size ($\chi^2 = 27.60$, df = 1, $p < 0.0001$; see Figure 2a;
164 also see Figure S1 for temporal consistency of proximity propensities across three years).
165 Population size ($\chi^2 = 6.33$, df = 1, $p = 0.012$) and family ($\chi^2 = 49.78$, df = 1, $p < 0.0001$)
166 significantly affected the extent of associating as well, with smaller populations (estimate ±
167 SD: -0.28 ± 0.07) and relatives (estimate ± SD: 0.50 ± 0.02) associating more prominently
168 than larger populations and non-relatives, respectively. Variation in dyadic configurations
169 with respect to sex, age and origin did not influence the extent of associating (all: NS).
170
171 **Proximity – Matched population comparison.** Population 3 and 4 were both characterized
172 by the absence of non-associated dyads (i.e., all possible dyads spent more or less time in
173 close proximity), yet they significantly differed from each other in terms of the *extent* to
174 which dyads associated (Permutation test: $\chi^2 = 50.24$, $p < 0.001$; mean ± SD twice-weight
175 association index group 3: 0.055 ± 0.066; group 4: 0.084 ± 0.054).
176
177 **Grooming.** The *probability* of two population members to engage in grooming with each
178 other significantly differed across populations (Binomial part LRT for "population": $\chi^2 =$
179 35.94, df = 1, $p < 0.0001$). In populations 1-4, the following proportions of all possible dyads
180 had a higher than 0 probability to be observed in a grooming interaction: 21.7%, 8.7%,
181 47.25%, 75.64%, respectively. This population-level difference could again be explained by
182 differences in population size (LRT "population size": $\chi^2 = 8.41$, df = 1, $p < 0.004$; estimate ±
183 SD = -2.82 ± 0.53; LRT "population": $\chi^2 = 0.14$, df = 1, $p = 0.713$). Dyads' age (LRT $\chi^2 =$
184 23.01, df = 2, $p < 0.0001$) and family configuration (LRT $\chi^2 = 127.38$, df = 1, $p < 0.0001$)
185 significantly affected subjects' likelihood to engage in grooming, with adults being more
186 likely to groom than dyads including sub-adults (estimate ± SD: adult-adult versus adult-
187 subadult: -1.33 ± 0.35, $p < 0.001$; adult-adult versus subadult-subadult: -3.08 ± 0.68, $p <$
188 0.0001), and relatives being more likely to groom than non-relatives (estimate ± SD: 3.77 ±

189 0.42, $p < 0.0001$). Dyads consisting of different configurations with respect to "sex" also
190 differed in their probability to engage in grooming ($\chi^2 = 6.03$, df = 1, $p = 0.049$), with male-
191 male dyads grooming with higher probability than female-female dyads (estimate ± SD: 1.16
192 ± 0.42, $p = 0.006$) and female-male dyads (estimate ± SD: 1.16 ± 0.420.81 ± 0.36, $p = 0.025$).
193 Female-male dyads and female-female dyads did not differ in their probabilities to groom
194 (estimate ± SD: 0.35 ± 0.27, $p = 0.203$). Variation in dyadic configuration with respect to
195 "origin" did not influence the probability of dyads to engage in grooming.
196 The *extent* to which dyads groomed was not significantly influenced by population
197 size ($\chi^2 = 0.092$, df = 1, $p = 0.761$; estimate ± SD: -0.079 ± 0.27), yet it was significantly
198 different for the four populations ($\chi^2 = 20.50$, df = 3, $p < 0.0002$; see Figure 2b; also see
199 Figure S2 for temporal consistency of grooming propensities across three years). Relatives
200 engaged in grooming more markedly than non-relatives ($\chi^2 = 29.71$, df = 1, $p < 0.0001$;
201 estimate ± SD: 3.77 ± 0.417). Different dyadic configurations with respect to sex, age and
202 origin did not influence grooming magnitude (all: NS).
203
204 **Grooming – Matched population comparison.** Population 3 and 4 were characterized by
205 significantly different *probabilities* to engage in grooming (LRT $\chi^2 = 6.39$, df = 1, $p = 0.012$;
206 group 3: 47.3%, group 4: 75.6% of all possible dyads established a grooming association).
207 Moreover, the populations significantly differed from each other in terms of the *extent* to
208 which dyads engaged in grooming (Permutation test: $\chi^2 = 26.82$, $p = 0.004$; mean ± SD twice-
209 weight association index group 3: 0.013 ± 0.025; group 4: 0.026 ± 0.032).
210
211 Taken together, the GLMM analyses yield the results depicted in Table 1.
212

Social Network Metrics.

Individual attributes. We permuted (n=1,000) the individually-derived social network attributes (SNas) across populations in order to assess whether individuals could be characterized as belonging to distinct populations by their magnitudes of network integration. The most obvious population differences, also taking into account the specific comparisons between the two populations matched in demography, were found for "reach" (grooming), "clustering" (proximity and grooming), and "affinity" (proximity). Figure 3 depicts the observed variation across all four populations (also see Tables S3 and S4).

Population-level properties. Population-level social network measures were calculated to investigate population differences beyond measures of individual social-integration and dyadic interactions. Clustering coefficients, modularity, and social differentiation scores can be viewed as indicators of population cohesion that are relatively robust against variation in population size (35). The network properties showed substantial variation across the four populations, with the highest clustering coefficient (i.e., cohesion) being ~3 times (proximity) and ~8 times (grooming) as large as the lowest one. The highest modularity (i.e., fragmentation) score was ~2 times (proximity) and ~1.7 times as large as the lowest one. The highest social differentiation (i.e., inequality of associations) score was ~2.8 times (proximity) and ~3.6 time as large as the lowest one (see Tables S5 and S6, and Figures S3 and S4).

Taken together, the individual- and population-level network metrics reveal significant differences in sociality between the study populations. On the level of individual integration, these differences are most pronounced with respect to reach, clustering coefficient, and affinity. On the population level, the differences are salient for all metrics assessed[1].

[1] The population-level metrics cannot be statistically compared because they represent single values per population

Discussion

Our investigation reveals the existence of substantial differences in sociality across neighboring populations of semi-wild chimpanzees that are not easily explained by socioecological theory and suggest the presence of culturally-learned interaction styles. Specifically, some populations proved more gregarious than others in terms of the size of their typical congregations throughout the day and their proclivities to associate and positively interact with others. Moreover, the relatively gregarious populations were characterized by network properties indicative of high social cohesion (Figure 4). Notably, neither ecology nor subspecies could be identified as explanatory mechanisms for the observed diversity, given that all chimpanzees lived in similar environments and populations did not systematically differ in ratios of subspecies (*nota bene* the most stringent comparison between populations 3 and 4 only comprised one subspecies). Furthermore, the population-level differences in gregariousness could not be fully explained by variation in population size and number of kin present, and the standardized method of data collection across populations precluded interference of group-specific procedural biases that have hindered previous comparative work. In conjunction, these results are consistent with the evolutionary anthropological conception of "culture" (i.e., larger between-group than within-group variation (36)), also because of their temporal stability (24), and thus suggest that at least part of the observed diversity in sociality across the studied chimpanzee populations might best be explained in terms of population-specific cultural styles of interacting.

The population differences with respect to individuals' propensity to congregate in variable party sizes were striking, especially for the populations closely matched in population size and demographic composition. Given the large enclosure spaces (averaging ~20,000m^2 per individual), spatial proximity out of necessity seems highly unlikely. Nonetheless, based on socio-ecological theory, we opted to control for population size in the estimation of the party size differences across populations, finding no indication to that effect. This suggests that individuals spontaneously exhibit population-specific tendencies to place themselves in contact with others, which was substantiated by corresponding population differences in the extent to which individuals associate with others, both in terms of proximity and grooming. The results from the social network analyses corroborate the findings following from the linear models, both concerning party size differences and rates of association. In particular, "affinity" (i.e., the extent to which one's neighbors associate themselves, thus representing a form of social embeddedness (35)) was highest in the

population with large average party sizes and strongest prevalence of associating. Furthermore, "reach" is a relevant measure for all sorts of transmission given that this measure captures the likelihood that individuals will interact with all population members. As such, high reach represents increased probability for transmission to occur, acknowledging that transmission (e.g., of information) requires spatial proximity (37). Based on our study, we hypothesize that some populations at Chimfunshi will have higher rates of information transmission than others. This hypothesis is warranted by the accompanying levels of population cohesion (clustering coefficients and modularity). Overall, the alignment of the results concerning party size, association tendencies, and network metrics provides credibility to the existence of significant population differences in chimpanzee sociality. Given that social closeness lies at the heart of many fitness-affecting behaviors, like cooperation (e.g., (38, 39)) and social learning (e.g., (17, 19)), we consider the reported differences in social interaction-styles (representing social closeness) meaningful, and encourage the study of the interplay between social climate and tangible behaviors more generally. Notably, the improbability of explanations in terms of ecological, subspecies or demographic variation additionally lends support to the conclusion that at least part of the documented variation in sociality is cultural in nature.

The search for cultural behaviors in primates has mainly been guided by the so-called method of exclusion (13, 21, 40). By ascertaining that population-specific behavioral phenotypes cannot be explained by non-cultural determinants (most prominently: ecology and genetics), causation in terms of social learning or culture is derived. This method has been criticized for its limited scope (i.e., populations often live in different ecological environments, hence ecology is difficult to "rule out" as explanatory factor (41)), and for the reason that culture should not be seen as a residual product of an elimination process, but as intricately connected with other determinants of behavior, like ecological affordances (34, 40). For instance, the selection of hammers for nut-cracking in chimpanzees may be afforded by the presence of suitable materials in their habitat, yet the choice for particular tools over others may be governed by population-specific custom (18). Nonetheless, when multiple, intraspecific populations are present in the same ecological environment, such as in this study, the method of exclusion gains power (21). In such a context, it presents a conservative approach to the identification of the cultural phenomenon.

An important challenge would be to explore whether socially-learned interaction patterns affect fitness at the individual or group level. In humans, multi-level selection has been invoked to explain within-group convergence in cooperative interaction styles which

enhance group survival in the context of between-group competition (42–44). Given its potential to align behavioral tendencies more rapidly than genetic evolution, culture plays a crucial role in this account (44, 45). The extent to which a similar explanation could hold for chimpanzees should be explored in light of the present study, and the evidenced cultural potential of chimpanzees more generally (15, 18, 27). For common marmosets, the emergence of population-specific behavioral styles (i.e., "group personality") was interpreted as a proximate mechanism to promote group-level cooperation, which in turn could boost individual-level fitness (3). The tendency for chimpanzees to cooperate in large parties (46, 47), even for targeted competition with neighboring groups (48), supports a multi-level selection explanation of population-level variation in chimpanzee interaction patterns. However, multi-level selection is considered to be one of the main drivers of the *unique* extent of human cooperation and pro-sociality (42, 45, 49), which should thus warrant a thorough scrutiny of its potential role in the evolution of the chimpanzee phenotype.

Proximately, the population differences in sociality could have emerged through the adoption of observed and/or experienced interaction patterns. Social learning has been robustly identified as within the range of capacities of chimpanzees (e.g., (15, 19, 20, 50)), and the exact mechanisms by which chimpanzees would learn from observed interaction-patterns need not be cognitively demanding ((51, 52) although see (53)). A similar case of interaction-style adoption has been reported with respect to reconciliation rates in a translocation experiment with macaques ((54), also see (55)). Moreover, by means of associative learning, chimpanzees could become psychologically predisposed to interact with future partners in line with previously experienced interaction-styles (e.g., with respect to the degree of gregariousness or tolerance) (56). The alternative explanation that the reported population differences are an artefact of management practices is unlikely for the reasons that the populations have not been formed discriminatively on the basis of gregariousness, and the handling procedures including food provisioning and interfering protocols (i.e., only when infants are very sick will there be interventions in the populations) are the same across populations. Moreover, all populations encompass both individuals with likely early trauma (wild born) and individuals that were born in the sanctuary, deeming the existence of population differences in sociality not easily explained in terms of variation in traumatized individuals (*nota bene* in the linear models, the effect of "origin" was controlled for). The influence of individual personality differences, however, has not been assessed in the current study. It may well be that the composition of personalities affect social network structure (e.g., see (57)). However, both the multi-level regression and social network analyses pointed

into the same direction with respect to the population-level differences in sociality, presupposing the workings of mechanisms that facilitate convergence from individual-level variation to population-level homogeneity (3).

Our findings are consistent with the identification of spontaneously emerged social climates in sperm whales (58). Based on measures of coordinated activity and association quality, sympatric sperm whales could be characterized by their clan-specific social interaction styles. Similar to the findings of the present study, some "clans" showed higher levels of dyadic sociality than others, which was associated with more homogenous relationships across dyads (58). A recent examination of intraspecific variation in social structure and dynamics in vervet monkeys reported population differences with respect to individuals' tendencies to preferentially interact with well-connected group members, and with respect to the stability of dyadic relationships (59). Despite the fact that these studies did not explicitly focus on identifying cultural variation (cf. (60)), in conjunction with the present study, these reports should spark further investigation of the presence of culturally-induced social climates in non-human animals. For instance, longitudinal studies are needed to examine whether such social climates persist, despite repeated changes in population composition (through e.g., migrations, births, and deaths). Similarly, translocation experiments in captivity could shed light on the extent to which local cultures influence the behavior of immigrants (e.g., see (54)). The latter approach would simultaneously enable the opportunity to study the mechanisms by which population-level homogeneity in interaction patterns could ensue (e.g., by means of conformity (18, 23, 61, 62), although see (63–65)).

The topic of behavioral diversity in non-human animals in general, and chimpanzees in particular (being one of human's closest living relatives), is both timely and pressing. Recent accounts have hinted at the possibility of substantial between-group variation in chimpanzees (28, 66, 67), despite the lingering species-typical view of "the chimpanzee" (see (46)). Notably, this variation need not be restricted to isolated traditions, like nut-cracking (18) or handclasping (20), but may be more fundamentally embedded in the very fabric of social interactions. Here, we show for the first time that neighboring chimpanzee populations can differ significantly in their social interaction patterns, while controlling for many factors that are hard to account for in a comparison of spatially distinct field-sites (e.g., food availability, climate, predation risk, but also influential scientific methods like data-collection protocols, sampling rates). Such population-specific interaction dynamics are important to recognize not only for acknowledging that results from experimental studies tapping into social behavior (e.g., social learning, prosociality, cooperation) may be biased by their

particular study-population, but also for pressing the need to incorporate a multi-population approach for obtaining an accurate species-representation for phylogenetic studies ((68), also see (59)). For instance, in tracing the evolutionary origins of human's extended forms of prosociality, based on the findings of the current study, it may be warranted to assess prosocial behavior in chimpanzee populations with differing magnitude of social dynamics, like the populations at Chimfunshi.

In more detail, as our closest living relatives, chimpanzees (and bonobos) are often times studied with the aim to learn whether certain human behaviors (e.g., cooperation, pro-sociality) might be derived or otherwise rooted in deeper phylogenetic history (69). This comparative approach – identifying contingencies and changes in evolutionary history by pinpointing similarities and differences across extant species – relies crucially on a correct characterization of any of the compared species. While the last years have witnessed a renewed interest in variation between human populations, and an increased recognition of the relevance to include this variation in any account of the human species as a whole, comparative psychology still often assumes the existence of a typical exemplar of a species without accounting for within-species variation (66). For example, there has been a series of opposing results concerning whether chimpanzees and humans vary in their active prosociality (70–74). One, as of today un-explored, possible explanation for these conflicting results is that the different groups of chimpanzees studied, *ceteris paribus*, vary in their tendencies to behave prosocially. Our data, we argue, promote a cultural comparative psychology that embraces within-species variation as a characteristic of the respective species, both in an aim to compare species fairly, and as a phenomenon worth studying comparatively in its own right.

Materials and Methods

Study system. Data were continuously collected from March 2011 to March 2013 at the Chimfunshi Wildlife Orphanage Trust, a chimpanzee sanctuary in Zambia. Subjects comprised 89 chimpanzees across four populations, living in forested enclosures ranging in size from 47 to 190 acres (see Figure S5). Chimpanzees at Chimfunshi stay outside overnight and only come indoors for supplemental feeding between 11.30–13.30. Except for a few meters along the fence line between groups 3 and 4, the chimpanzees do not have visual access to each other. Approximately half the chimpanzees were wild-born and integrated into peer groups at the sanctuary, the other half were mother-reared at the sanctuary. Groups 1-4 were formed between 1984–1989, 1990–1994, 1995–1999, and 2000–2002, respectively. For demographic details of the chimpanzees under study, see Table S2.

Data collection and operational measures. Data collection across all populations was standardized by adhering to one focal follow protocol (75). Subjects were quasi-randomly selected as focal subject by a trained observer (E) starting at one of 4 (one of 7 in the two larger groups) pre-assigned locations surrounding the enclosure and selecting the subject closest to the start location. Subjects were video-recorded (centered with a 2-meter radius) continuously for 10-min. If the focal moved out of sight, data were only included when the total time the focal was in view exceeded 5 minutes. At the end of each focal follow, one scan sample was obtained by E panning from left to right. All chimpanzees observed during the focal follow and scan sample were counted to belong to the focal's party composition. The next focal chosen was the closest chimpanzee to the previously recorded focal. Observations were done for one hour every day, alternatingly between 8:30-11:00 and 14:00-16:30. Only one video per subject per week was randomly selected to increase data independency, resulting in a total of 3002 focal follow videos for analysis (group 1-4, n=765, n=911, n=635, n=691, respectively).

From the videos, we derived party size and coded proximity, grooming, play, aggression and copulation using a standard chimpanzee ethogram (adapted from (76)). Party size was defined as the sum of individuals within a focal's party composition (including the focal). Proximity was defined as being in a 1-meter radius of the focal individual; direct passings within a 1-meter radius (without a moment of paused locomotion), grooming or aggressive encounters were excluded from this category. Grooming was defined *sensu* Nishida et al. (76) and counted both when the focal provided or received grooming (i.e.,

directionality not considered here). Play, aggression and copulation were also defined *sensu* Nishida et al. (76), with the restrictions that interactions required physical contact (to minimize ambiguity). Per day, a 1/0 sampling method was used (for each behavior coded) to further maximize data independency (35). Prior to coding the videos, all members of the coding team demonstrated high inter-observer reliability with a lead coder (Cohen's kappa ≥ 0.85). Videos were coded in INTERACT (Mangold International GmbH) and Excel. Party size, proximity and grooming (given and received collapsed) were measures with sufficient data for analysis (n=3002, n=6064, n=946, respectively); play (n=246), aggression (n=10) and copulation (n=17) were observed too infrequently for reliable between-population comparison.

Social network indices were calculated with SOCPROG (77). First, we extracted twice-weight association indices (35), both for the proximity and grooming data. The twice-weight index was chosen as it is the least biased when there is an increased possibility of observing individuals who were associated over those alone ((78) also see (79)). The twice-weight association index (AI) is calculated as:

$$x/(x + 2y_{AB} + y_A + y_B)$$

where x = the number of sampling periods (days) in which individual A and individual B were associated, y_A = the number of sampling periods in which only A was identified, and y_B = the number of sampling periods in which only B was identified, and y_{AB} = the number of sampling periods in which both A and B were identified but not associated with each other. "Identified" refers to an individual being captured on video that day, either as a focal subject or as present in the subgroup of another focal subject.

Second, for their relevance to individuals' social integration, the following social network attributes (SNas) per individual were extracted, both for the proximity and grooming data: Strength, Eigenvector-centrality, Reach, Clustering-coefficient, and Affinity (see Table S7). Additionally, for their relevance to group sociality beyond the dyad, and comparability across groups when sampling methods are identical (35), as in our case, the following population-level social network measures were extracted: clustering coefficient, modularity (based on eigenvector method, calculated from gregariousness (80)), and social differentiation. Clustering coefficient is a measure of group cohesiveness, encapsulating the extent to which connected individuals are themselves connected to others (81). A relatively large clustering coefficient corresponds to high group cohesion. Modularity represents group

fragmentation and can be viewed as a measure of subgroup division (81). As such, a relatively large modularity score corresponds to low group cohesion. Social differentiation is a measure of variability in probability of association among dyads (35). Hence, a relatively large value corresponds to a relatively unequal distribution of associations across group members.

Lastly, given that socio-ecological theory predicts that social behavior could potentially vary depending on population size (82, 83), and that results from social network analysis may be affected by the number of individuals interacting (35), we present all results separately for two populations highly matched in demography (e.g., population size, composition in terms of sex and age; see Table S2), but also in enclosure size and subspecies.

Data analysis. First, party size differences between populations were analyzed with Generalized Linear Mixed Models with Poisson error distribution and log link function (lme4 package: (84)). The full model consisted of the fixed effects origin (wild/sanctuary born), rank (*z*-transformed), age and sex. Additionally, to account for potentially meaningful differences in population demography, we included population size and number of family units (both log-transformed) as fixed effects (i.e., assuming direct link with party size). Subspecies variation was minimal (i.e., almost all chimpanzees were found to belong to the subspecies *troglodytes schweinfurthii*, see Table S2) and thus could not be modeled for its effect on party size[2]. Focal follow duration was included as offset term to control for observation effort. We included the random intercepts for focal, day and population-identity, and the random slopes for rank and age nested in day. To test the temporal stability of any population effect, we further included the random slopes for year (2 dummy coded and centered variables derived from the years 2011, 2012 & 2013) within population. The null model resembled the full model, except for the omission of the random effects for "population-identity". The effects of population-identity (including "year within population") were tested with Likelihood Ratio Tests (henceforth LRT: (85)).

Second, social network indices were analyzed with Hurdle models (for AIs, to accommodate the numerous zeros reflecting absence of association) and permutation tests (for SNas). The Hurdle models consisted of a Binomial part (logit link function) to model the likelihood of presence/absence of association, and a Gamma part (log link function) to model the non-zero AIs. Both model types consisted of the fixed effects dyad.sex (female-female, male-female, or male-male), dyad.age (subadult-subadult, subadult-adult, or adult-adult), and dyad.origin (wild-wild, wild-sanctuary, sanctuary-sanctuary). For its potential effect on the

[2] For the same reason, we excluded subspecies information from all further analyses.

tendency of two group members to associate, we included population size (log-transformed) as inverse offset term (i.e., offsetting the decreased opportunity to associate with each individual with increasing population size). Instead of number of family units, here, we added a variable denoting whether or not the dyad was between family members (same.matriline yes/no) as fixed effect. Furthermore, we included the random intercepts of population-identity, focal and partner, including all possible random slopes within focal and partner (86, 87). The full models were compared with reduced models (LRT: (85)) to assess the effect of population-identity. For the SNas, we permuted (n=1,000) population identity across individuals to test the likelihood that obtained network indices were indistinguishable from a random distribution across populations. Given the complexity of social dynamics in chimpanzees, and our decision to use only one focal follow per subject per week for increased data independency, to obtain reliable SNas, we used all data for computing the respective social network metrics (see Table S7) instead of parsing the data across the three data-collection years, hence precluding any stability-across-time analysis.

All models were fitted in R (version 3.3.3: (88)) using the functions lmer and glmer of the R package lme4 (version 1.1-12: (84)). We considered *p*-values less than 0.05 as significant, and corrected for multiple testing using Bonferroni-Holm corrections (89).

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Figure legends

Figure 1. Party size across four neighboring populations of semi-wild chimpanzees 2011-2013 (population 1-4: n=765, n=911, n=635, n=691 observations, respectively). Medians are represented by the bold, horizontal lines within the boxes. The boxes represent the interquartile range (IQR), the vertical lines attached to the boxes represent Q1-1.5 IQR (lower) and Q3+1.5 IQR (upper).

Figure 2. Dyadic a) proximity and b) grooming associations per population. The association values (black dots) are the twice-weight indices ($x/(x + 2y_{AB} + y_A + y_B)$) for all dyads (population 1-4: n=300, n=1081, n=91, n=78, respectively). Medians are represented by the bold, horizontal lines within the boxes. The boxes represent the interquartile range (IQR), the vertical lines attached to the boxes represent Q1-1.5 IQR (lower) and Q3+1.5 IQR (upper).

Figure 3. Social network attributes across the four study populations. Significant differences ($p <$ 0.0001) were found for all attributes except "Strength", some of which were between the larger and smaller populations (e.g., eigenvector centrality), others independent of population size (e.g., clustering coefficient), also see Table S3 and S4. Ranges are represented by the boxes (IQR), medians are indicated by the bold, horizontal lines within the boxes.

Figure 4. Visual illustration of population differences in sociality across the four populations at the Chimfunshi Wildlife Orphanage. The icons refer to the following characteristics of each group: Party Size, Proximity, Grooming, Clustering, Modularity and Social differentiation. Proximity and Grooming represent the aggregation of all dyadic twice-weight association indices. Clustering, Modularity and Social differentiation represent population structure in terms of social cohesiveness, based on proximity. The height of the grids indicates the range of a given characteristic across the four populations. The position of each icon on the grid's vertical axis indicates the relative position of the group in relation to the total range of the characteristic across all populations.

Supporting Information (SI)

Figure legends Supporting Information

Figure S1. Proximity (means per group per year). The absence of significant interaction between population and year ($\chi^2 = 0.11$, df = 6, $p = 0.86$) corroborates the temporal consistency of variation in social culture across the four neighboring populations of chimpanzees at Chimfunshi. Medians are represented by the bold, horizontal lines within the boxes. The boxes represent the interquartile range (IQR), the vertical lines attached to the boxes represent Q1-1.5 IQR (lower) and Q3+1.5 IQR (upper).

Figure S2. Grooming (means per group per year). The absence of significant interaction between population and year ($\chi^2 = 2.89$, df = 6, $p = 0.29$) corroborates the temporal consistency of variation in social culture across the four neighboring populations of chimpanzees at Chimfunshi. Medians are represented by the bold, horizontal lines within the boxes. The boxes represent the interquartile range (IQR), the vertical lines attached to the boxes represent Q1-1.5 IQR (lower) and Q3+1.5 IQR (upper).

Figure S3. Social networks for the two chimpanzee populations matched in demographics and subspecies (*a* = population 3; *b* = population 4), based on twice-weight proximity association indices ($x/(x + 2y_{AB} + y_A + y_B)$). Nodes represent individuals, the lines (edges) between nodes are weighted by the strength of their association. Edge-weights are comparable across populations; edge-weights < 0.1 not shown for either population to improve clarity. Nodes are sized based on their weighted strength ($\sum_J a_{ij}$). Nodes representing females are green, nodes representing males are orange, with the exception of the alpha males, which are blue.

Figure S4. Social networks for the two chimpanzee populations matched in demographics and subspecies (*a* = population 3; *b* = population 4), based on twice-weight grooming association indices ($x/(x + 2y_{AB} + y_A + y_B)$). Nodes represent individuals, the lines (edges) between nodes are weighted by the strength of their association. Edge-weights are comparable across populations; edge-weights < 0.1 not shown for either population to improve clarity. Nodes are sized based on their weighted strength ($\sum_J a_{ij}$). Nodes representing females are green, nodes representing males are orange, with the exception of the alpha males, which are blue.

Figure S5. Aerial view of the habitats of the four chimpanzee populations under study (at the Chimfunshi Wildlife Orphanage). Numbers in circles represents population identity.